

Concluding Remarks: On the Difficulty to Reconcile Theories with Facts

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Summary

Using the example of two species of waterfleas that have coexisted for at least half a century in a small subalpine Bavarian lake, the multiplicity of simultaneously effective mechanisms of coexistence is discussed. At least ten mechanisms are postulated to be of importance, virtually all of them have one or more counterparts in the real system. The need is stressed to derive general theories about the coaction of many basic principles.

The idea of this symposium was to offer a selected scope in the field of population ecology. Yet the array of data, theories and views put forward has turned out to be so wide that it would be near-impossible and unjust to the contributions of many speakers to attempt a summary of «communiqué» expressing the essence of the meeting. There were very basic and general models (MAY), and quite complex and specific ones (CLARK and HOLLING); we had studies on the properties of individuals in order to explain the behaviour of a whole population or even the interaction between populations (HALBACH, KAISER). A number of papers were straightforward population studies (SINGER and EHRLICH, PULLIAM and PARKER) including genetic aspects (KREBS), others concentrated on competition and/or predation (KERFOOT and PETERSON, CODY, MURDOCH, HASSEL), some vigorously defending the principle of exclusion (DIAMOND) or coexistence (ROUGH-GARDEN, CODY, CASE, ROSENZWEIG), others challenging the offered evidences (BIRCH). Finally, some contributions dealt with complex multi-species systems (GILPIN and MCCLELLAND, ZWÖLFER, DEN BOER).

Despite of this breadth of facts and ideas we excluded several important aspects. On the taxonomic side, for instance, we carefully avoided *higher mammals*, especially primates. With their highly complex social interactions, they would have tremendously complicated the discussions during these four days. – We did not consider the vital problem of *population borders*. Their dynamics differ very markedly from those of classic populations: In a steady-state situation, dispersal produces permanent marginal subpopulations above the K-level (mortality > birth rates) which cannot maintain themselves. They are continuously fed by more central sustaining regions which therefore must be below the K-level (birth rates > mortality). Depending on the power of dispersal and the effective population size, such sustained and sustaining non-K subpopulations may be more normal and more important than the classic populations considered in most models. – We never challenged the *concept of the population* itself, perhaps with the notable exception of DEN BOER's contribution. There are indeed numerous systems, for instance long narrow continua along coasts, oceans with different horizontal water movements in different depths, migrating insects, birds and mammals, nomadic primate groups, or hybrid swarms, where the

conventional concepts of populations may be misleading rather than helpful. – The topic of *succession* which almost automatically comes to mind when competition is mentioned, was generally omitted.

If these and other domains of population ecology were not treated in this symposium, it was not because we were unaware of them; rather it has to do with how much condensed information one can present and assimilate in a given stretch of time. I think we used our time properly.

If I were asked to name an identifying criterion, a key character of this symposium, I would venture to propose that a really striking feature was the great divergence of views, and – at least this is my impression – a partial incompatibility of the presented data and theories. It is on this theme – the difficulty to weld together theory and facts – that I should like to enlarge a bit. I am going to use as an example some data and ideas about competition and coexistence which our group in Munich has gathered during the last years. I shall try to juxtapose expectations on the basis of principles known to influence coexistence, and facts from field and experimental data. The contributions of E. BOHL (1974 and unpublished data), M. KRÄMER (1978, unpublished data), V. KUCKLENTZ (1975), C. SCHMELZER (1976) and A. SEITZ (1977) are particularly appreciated.

The system we studied is relatively straightforward: A beautiful subalpine postglacial lake, the Klostersee in Southern Bavaria, and 2–3 species of very similar water fleas which use essentially the same algal and bacterial food and are exposed to the same piscine enemies. The water fleas – *Daphnia hyalina*, *D. cucullata* (and more recently, also *D. galeata*) – are fairly simple animals, not quite as molecular as rotifers, still simple enough to attract theoreticians but probably too simple to be regarded as animals by primatologists.

The principal question we asked was why two quite similar species of *Daphnia* have coexisted in the Klostersee for at least 50 years, probably much longer. If seasonal and other short-term fluctuations are disregarded, there was indeed a fair constancy of numbers over a considerable span of time, a semipermanent *status quo* (for literature, see JACOBS, 1977b). What principles, theories or hypotheses do we have to invoke if we wish to explain extended coexistence? In the following I am going to list ten such principles which might apply in the Klostersee situation, in a headline fashion. None of them needs to be permanently effective but each may be important under certain circumstances. They may apply to each species independent of the other, or they may be based on interactions between both species.

First I shall consider factors that do not guarantee a stabilized coexistence but nevertheless evoke or facilitate the maintenance of a given situation. Such factors should have equal footing with truly self-stabilizing factors, opportunistic animals do not insist on the perfection we ecologists would like to see.

1. A *stable, non-changing environment* can be very helpful for a long-term constancy of species composition. This is trivial but it works.
2. Longevity of individuals relative to the rate of environmental changes. In the case of *Daphnia* this would include the production of long-lived resting eggs. In combination with overlapping generations which insure a richness of age classes in each environmental situation, longevity could produce a considerable long-term inertia of population size.
3. *Spread of risk*: By tying various life functions to different environmental factors that fluctuate independent of each other, perhaps randomly, or even in an antagonistic fashion, a population may achieve the constancy of a good insurance company (DEN BOER, 1971).

4. There is of course always the possibility of *permanent random colonization* from other populations to maintain a multi-species system. This would be analogous to the maintenance of genetic polymorphisms by continuous introgression.
5. *Short-term changes in fitness*, for instance, in relation to seasons. Environmental fluctuations could produce adaptive changes in individuals or variations of gene frequencies in populations which could have a stabilizing effect.
6. Tendencies to *equalize the fitnesses* of competing species. In the classical N_1/N_2 -plot this would mean an overlap of isolines of equilibrium. The result would be an indifferent equilibrium. It could be achieved by two methods: two species may become more or less identical so that only random drift could evict one or the other from the system. This would be analogous to the maintenance of neutral or equally fit alleles in a population. It might also be accomplished by *compensatory actions* of different fitness components such as survival, fecundity, success of finding a sexual partner, or speed of development (JACOBS, 1977a).

In contrast to these factors which do not have any properties of self-stabilization, we have to consider *negative feedback mechanisms* which tend to bring about a permanently stabilized situation, in other words, abundance-dependent mechanisms. I shall mention only the most fundamental ones:

7. *Classical niche separation* (including complete independence of both species). This may include temporal or spatial segregation. The contrast to the idea of overlap or identity of niches (pt. 6) should be noted.
8. *Spatial or temporal overlap* if a mutual or one-sided benefit is involved. For instance, a partner may be welcome as an attractive alternative prey. Or, analogous to Müllerian mimicry, two species might wish to cooperate to swamp a satiable common predator by sheer numbers to minimize the per capita mortality.
9. *Relative-abundance-dependent predation* (for instance, by fish, cf. MURDOCH et al., 1975). Under certain circumstances, this mechanism may switch a competitive situation into a mutualistic one.
10. *Abundance-dependent dispersal* to other sites.

These 10 factors are certainly not all one can think of but they are enough to confuse one if they apply to one ecosystem at the same time, and if they are subject to simultaneous natural selection.

Now, in contrast to these potentially effective principles, a few facts about the *real* system, and some suggestions that come from these facts:

1. Within a distance of about 10 kilometers around the Klostersee, there are more than 20 lakes, and more than half of them are or have been inhabited by *D. hyalina* and/or *D. cucullata*. The amount of cladoceran exchange between these lakes is not known but it is conceivable that coexistence in the Klostersee is in reality a *multi-lake affair*. We hope by using electrophoretic techniques to gain some insights into the genetic identities of the lakes with respect to *Daphnia*.
2. Both species are usually parthenogenetic but at times they produce males and fertilized *resting eggs*. The production of such eggs is known to depend on animal density, food scarcity, temperature, and relative day-length (BANTA, 1939; MORTIMER, 1936; STROSS, 1966). These factors are partly abundance-dependent, partly independent. The eggs may rest for months or years. We do not know how much this factor contributes to coexistence mainly because we have difficulties to judge which portion of, say, a spring population comes from last year's resting eggs.

3. Both species exhibit *compensatory fitness components*: The somewhat larger *D. hyalina* has a higher birth rate, and hence, a higher intrinsic rate of natural increase, and a higher K-value than the smaller *D. cucullata*. This is true for a wide range of temperatures and food levels (SCHMELZER, 1976). Thus the species conform to the size-efficiency hypothesis (HALL et al., 1976). *D. cucullata*, on the other hand, has a mortality advantage: Most mortality in the Klostersee is due to predation by fish, and fish prefer *D. hyalina* because it is, on the average, larger and more opaque than *D. cucullata*. Hence, the smaller *D. cucullata* is able to compensate its reproductive disadvantage by an escape advantage (JACOBS, 1978).
4. Since there is an alternation of seasons with much food but few enemies in spring, and much predation but little food in late summer, the differential adaptation of the species to reproduction and escape produces a *seasonal segregation of the abundances*: *D. hyalina* is more abundant in one season, *D. cucullata* in the other (JACOBS, 1977b). This temporal segregation could amount to a classical niche separation with respect to food because there is also a seasonal succession of food species as evidenced by changes in the composition of chlorophyll types (SEITZ, 1977).
5. There is not only the stabilizing antagonism of reproduction vs. mortality but also a compensatory mechanism within the reproductive scheme itself: The larger egg-bearing females of *D. hyalina* are usually found a few meters deeper in the lake than the somewhat smaller females of *D. cucullata*. During thermal summer stratification, *D. cucullata* females are warmer than *D. hyalina* females. SEITZ (1977) has shown that these temperature differences of the poikilothermic animals may compensate and even over-compensate the intrinsic disadvantage of *D. cucullata*: at certain times of the year, warm *D. cucullata* may actually reproduce faster than cold *D. hyalina*!
6. The differential mortality by predation is enhanced if both species are *simultaneously* in the range of a fish's vision. KRÄMER (unpublished data) has shown experimentally that planktivorous minnows (*Phoxinus phoxinus*) may neglect a small prey if a larger prey is at hand, even if the larger one is so far away that the image on the retina of the fish is smaller. From other fish species it is known that they select by apparent rather than absolute size (O'BRIEN et al., 1976). These data suggest that it might be a good strategy for the smaller *D. cucullata* to seek *spatial overlap* with the larger *D. hyalina* during the season of dying when «competition for enemies» is dominating. On the other hand, *D. cucullata* might wish to seek *spatial segregation* during the season of reproduction if there is competition for food.
7. We have very strong evidence that selective feeding of fish on *Daphnia* depends not only on size and species, and of course on light, but also on the relative abundance (KUCKLENTZ, 1975; SEITZ, 1977; BOHL, unpublished data). At least two mechanisms appear to be involved: First, both prey species have, as I mentioned before, a somewhat different vertical distribution. Fish may select the depth level in the lake with the densest total prey population, which would probably be dominated by the most abundant species. Second, within a given depth level, minnows have been shown by KUCKLENTZ to switch to the most abundant cladoceran prey species even if these are relatively small (KUCKLENTZ, 1975). Thus far, the mechanisms of this switch are obscure.
8. Size-selective feeding of predators leads not only to differential mortality, but indirectly also to a differential birth rate. The reason for this is that the largest animals which are preferentially eaten are the best reproducers. Thus the predation disadvantage of *D. hyalina* is a double one: its intrinsic advantage, viz. its reproductive capacity, is also handicapped by predation. This secondary effect of size-selective feeding on reproduction had a significant stabilizing effect in laboratory experiments where a

mixture of both competitors was exposed to fish: The higher the relative abundance of the larger species, the stronger was the relative depression of its birth rate (JACOBS, 1978).

9. *Both species are cyclomorphic*, i.e. they show seasonal oscillations of their phenotypic appearance in successive generations. The most striking morphological changes concern the development of a helmet and the elongation of the caudal carapace spine in summer. The phenomenon is very striking in *D. cucullata*, less conspicuous in *D. hyalina*. It is mainly controlled by environmental factors (for summarizing reviews see JACOBS, 1961; DODSON, 1974; JACOBS, 1979) but natural populations are also genetically polymorphic with respect to cyclomorphosis, and at least in cyclomorphic rotifers, a seasonal succession of different genotypes has been suggested (DE BEAUCHAMP, 1952; HALBACH and JACOBS, 1971; KING, 1979). A wealth of data indicates that rotifer and cladoceran cyclomorphosis influences the ability to escape predators (e.g. GILBERT, 1967; HALBACH, 1971; ZARET, 1972; ZARET and KERFOOT, 1975; JACOBS, 1967, 1979). It would be curious if cyclomorphosis in the Klostersee was adaptively neutral.
10. HEBERT (1974) has shown that in some English lakes small populations of *Daphnia* exhibit marked *seasonal changes of gene frequencies*. The causes are still obscure but there is a distinct possibility that in some lakes such changes could also be related to abundance. We plan to do similar studies on *D. hyalina* and *D. cucullata*.

The story of these two species in the Klostersee should be complicated enough by now. Virtually all of the mechanisms that can be postulated from a theoretical standpoint have one or more counterparts in the reality. Now the obvious questions: Which of these multiple mechanisms contribute how much to the observed long-term coexistence, and how are the interactions? Do we really need negative feedbacks to explain 50 years of coexistence? Is it a meaningful approach to single out one, two, or three mechanisms as «the» important ones (we have at least some evidence [JACOBS, 1977b; SEITZ, 1977] that in different years different mechanisms carry a different weight)? How important are third and fourth competitor-prey species? And ultimately, how should we formulate an integrated model or theory? One could of course attempt to build a specific theory around the Klostersee situation. At worst it would be a simulation in its verbal sense, i.e. it would imitate the reality but not represent it. At best it would be a correct causal explanation of this particular system. But the satisfaction for the ecological generalist would be small in either case. What we expect of theories is general applicability. What then should we do? With this question I come to the moral of the story – this is how German fairy tales usually end.

We need generalizing theories on the multiple coaction of principal mechanism. I believe that there is some danger in it to restrict our theoretical thinking to simple mechanisms extremely useful as they are. Even seemingly straightforward real systems are not as unsophisticated as we may hope. I did not expect the Klostersee to become that complicated. By extrapolation I have to accept that population systems involving higher animals like birds, monkeys, and man, will have difficulties even with our more complicated models, and it is not the fault of the populations but of the models.

To be true, there are numerous publications of complex causal models involving many sub-mechanisms but virtually all of these are tailored to fit a specific real system or even a single species in its environmental frame (see, for instance, the contribution of CLARK and HOLLING in this volume). What we lack are generally valid complex theories. There are some tentative and fruitful approaches to this, in part already quite old, like the coaction of competition and predation, the combination of stochastic and deterministic elements, the

combination of abundance-independent spread of risk and abundance-dependent feedbacks, and more recently, the combination of genetic fitness concepts with ecological models. But all these attempts, even very sophisticated ones (cf. SMITH, 1974; MAY, 1976) usually do not involve more than a few sub-mechanisms. This is really in contradiction to natural systems. I think it would be important to know something general about the ways in which *numerous* basic principles rather than two or three cooperate, under which circumstances which components are most likely to dominate, which ones can be discounted in the presence of certain others, and how one mechanism modifies the others. Is it possible at all to formulate *complex yet generally valid* rules on such coactions? If yes, are they worth anything, or would they offer too many options to be meaningful? I must confess that presently I am somewhat at a loss how to cope with this problem – the discrepancy between generalizing theory and complex reality – in a constructive way. This is then perhaps a good time to end – a certain degree of perplexity may be a good catalyst for future insights.

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